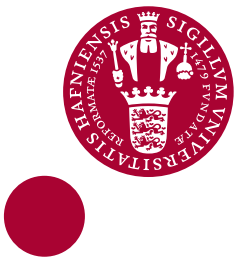

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Review

Nutritional Dimensions of Invasive Success

Jonathan Z. Shik[1,2,*] and Audrey Dussutour[3,*]

Despite mounting calls for predictive ecological approaches rooted in physiological performance currencies, the field of invasive species biology has lagged behind. For instance, successful invaders are often predicted to consume diverse foods, but the nutritional complexity of foods often leaves food-level analyses short of physiological mechanisms. The emerging field of nutritional geometry (NG) provides new theory and empirical tools to predict invasive potential based on fundamental and realized nutritional niches. We review recent advances and synthesize NG predictions about behavioral traits that favor invasive establishment, and evolutionary dynamics that promote invasive spread. We also provide practical advice for applying NG approaches, and discuss the power of nutrition to achieve a more predictive invasion biology that explicitly integrates physiological mechanisms.

Highlights

Species invasions represent a global threat to biodiversity.

Preventing invasive species requires an ability to accurately predict future invaders. Diet breadth analyses are often used, but the nutritional complexity of most foods means that food-level analyses tend to lack explicit physiological mechanisms.

The emerging field of NG can strengthen physiological predictions based on niche-based mechanisms governing invasive potential.

We use NG to synthesize predictions of behavioral traits that govern invasive establishment and evolutionary dynamics that govern invasive spread.

We also provide practical tools for applying the NG toolbox in the laboratory and in the field, and we suggest how invasion biologists can use these approaches to integrate insights from disciplines as diverse as comparative genomics and applied animal husbandry.

Moving from Food-Level to Nutrient-Level Predictions about Invasive Potential

Biological invasions threaten the planet's biodiversity in ways that far exceed short-term economic and public health impacts [1–4], with invasive species implicated in 25% of plant extinctions and 33% of animal extinctions [5]. Nevertheless, our ability to identify and potentially prevent the most likely future invaders is often constrained by incomplete ecophysiological knowledge. For instance, in most cases we cannot readily link the intrinsic physiological requirements and tolerances of potential invaders [i.e., **fundamental nutritional niches** (FNNs); see Glossary)] to the availability of foods in introduced habitats that satisfy these FNNs (i.e., **realized nutritional niches**, RNNs). The emerging field of **nutritional geometry** (NG) can be used to make these links and thus provides a new research agenda for unlocking greater predictive power in the field of invasion biology [6–8].

Broad diets in animals and broad soil-quality tolerances in plants have classically been thought to predict the ecological generalism that governs invasive success [8–11]. However, although food-level estimates of diet breadth and qualitative descriptions of soils can be correlated with sustained population growth over large areas [12–14], they can provide an incomplete picture when making general predictions about the invasive potential of novel species [15–17]. This is because foods are complex mixtures (macronutrients, micronutrients, recalcitrant compounds, toxins, water, etc.), and nutritionally ambiguous dietary estimates based on catalogued prey items (e.g., [18]) or stable isotopes [19–21] may be weakly linked to the actual physiological mechanisms that govern invasive success [22].

For instance, seemingly similar foods can have different nutritional compositions, even within narrow taxonomic groupings of animal prey items (Figure 1A) and plant hosts (Figure 1B), and even among tissues within individual animal prey [23–27] (Figure 1C) or individual plants [28–31] (Figure 1D). One example is the invasive wolf snail (*Euglandina rosea*) which consumes other snail species [32] that vary widely in their macronutrient composition from a protein (P) to carbohydrate (C) ratio of 2:1 P:C in the giant African snail (*Achatina fulica*) to 30:1 P:C in the garden snail (*Helix aspersa*) [33]. Species can also partition a single resource pool in nutritionally cryptic ways such that food intake may fail to predict nutrient intake [31], such as with the invasive cypress aphid (*Cinara cupressi*) that exploits a nutritionally diverse range of feeding sites on its host, from young leaves to woody stems [34]. Dietary specialists can also be successful invaders if

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they can exploit RNNs in new habitats that target their narrow FNN dimensions, for example when the invasive range of the specialist fungal parasite *Aphanomyces astaci* expanded with its invasive crayfish host [35]. These examples highlight that food-level estimates of resource opportunity [36,37] can be incomplete without nutritional data.

NG builds upon food-level analyses to consider nutrients when predicting invasive success by providing practical tools to link nutritional niche dimensions with ecological performance and evolutionary fitness [7]. This framework further allows researchers to consider interactions among multiple food components, which is valuable because organisms are typically limited by more than one nutrient at a time. Indeed, NG studies have repeatedly shown that organisms from slime molds [38] to humans [39,40] simultaneously regulate multiple nutrients (e.g., proteins, carbohydrates, lipids; i.e., **nutrient regulation**) when foraging in laboratory experiments and in natural field conditions [41]. Recent advances also provide powerful graphical tools to visualize this nutritional colimitation, and a theoretical framework to explain the variation in terms of 'Hutchinsonian' fundamental and realized niches [8,17]. These nutritional niche dimensions have further been linked to traits governing invasive success, including the capacity to resist environmental stress [42] and express behavioral aggression [43,44].

Using NG To Predict Invasive Potential

NG provides experimental approaches to visualize the tradeoffs that organisms are willing to make to maintain **nutritional homeostasis** [7]. The nutritional state of an organism is represented as a moving point in a multidimensional **nutrient space**, and changes over time with intake, metabolism, growth, reproduction, and excretion (Figure 2). The optimal state that maximizes fitness is represented as an **intake target** in the same space (Figure 2A). Each food is a vector, or **nutritional rail**, that is determined by the X:Y ratio of nutrients it contains (Figure 2A). As the organism eats, its nutritional state changes along the vector of the consumed food rail. If two or more complementary foods are available, the organism can achieve its intake target by mixing its intake from the different foods (Figure 2B). Although a nutritionally balanced diet enables the organism to reach its target, an imbalanced diet forces it into a compromise between overingestion of some nutrients and underingestion of others (Figure 2C). By confining the organism to a range of single diets with different macronutrient ratios, we can define behavioral **rules of compromise** that can be used to place species on a continuum between nutritional generalists and specialists (Figure 2D). We can also test whether organisms can defend their intake target by adjusting foraging to compensate for the ratios of nutrients and/or the overall concentrations of these nutrients in available foods (Figure 2E). Researchers can visualize these behavioral feeding responses both in controlled laboratory feeding experiments with nutritionally defined diets and in observational field studies of freely foraging animals, yielding intake arrays showing the consumption of different nutritional ratios and concentrations (Figure 2F).

We can use NG to predict invasive potential in two steps. The first involves measuring a propagule's foraging and consumptions strategy when confined in a no-choice laboratory feeding experiment to a wide range of nutritionally defined diets with different nutritional ratios and concentrations (Figure 3A). We can then visualize the propagule's FNN by measuring variation in its growth, survival, fitness, etc. across this **performance landscape** (Figure 3B). The next step involves building upon more traditional food-level approaches to define the RNN of an organism by observing how it navigates a real performance landscape in nature (Figure 3C). This requires field work to identify and catalogue actual harvested foods, and then laboratory work to quantify the nutrient composition of these foods [16,45,46]. By overlaying field-based RNNs upon laboratory-based FNNs, we can test whether and how organisms can target their intrinsic FNN dimensions following introduction (Figure 3D).

Glossary

Fundamental nutritional niche (FNN): a region of nutritional space in which survival, growth and reproduction are possible, that reflects physiological tolerance and constraints, and is typically measured under controlled conditions in the laboratory.
Intake target (IT): the point in the nutrient space where fitness (or performance) is maximized, and against which overingestion or underingestion of nutrients can be inferred.
Nutrient regulation: the ability of an organism to maintain nutritional homeostasis when its foraging is restricted to imbalanced diets, through a combination of selective ingestion, assimilation, or excretion.
Nutrient space: a multidimensional space in which each axis represents a food component (e.g., macronutrients, micronutrients, toxins, etc.).
Nutrient tolerance: reflects the breadth of the FNN of an organism and is mediated by traits for surviving under physiologically stressful conditions of nutrient imbalance or scarcity.
Nutritional geometry (NG): a theoretical and empirical toolbox for visualizing and modeling the tradeoffs that organisms are willing to make to maintain nutritional homeostasis (also called the geometric framework).
Nutritional homeostasis: a process by which an organism adjusts its feeding behavior and its post-ingestive physiology to balance nutrient intake, assimilation, and expenditure.
Nutritional landscape: the foraging environment that an organism must navigate to acquire foods that vary in nutrient ratios and concentrations, and upon which performance can be quantified and niche breadth can be visualized.
Nutritional rail: a diagonal vector in nutrient space that represents a particular food, and where the slope indicates the balance of nutrients (ratio and concentration) contained in the food.
Realized nutritional niche (RNN): region of nutrient space containing foods that an organism actually consumes in the presence of competition and predation, and that is typically measured in the field based on nutrients contained in foods harvested by the focal organism.
Rule of compromise: the foraging tradeoff between overingesting some

Nutritional Dimensions Governing Invasive Establishment

The concept of the multidimensional nutritional niche and its relevance to invasion biology was recently introduced [8], with the suggestion that generalism of food composition and food exploitation might govern invasion success. Based on the conceptual framework developed in Figure 2 and the practical approaches highlighted in Figure 3, we expand upon this paradigm by synthesizing a novel suite of testable NG predictions about the behavioral mechanisms governing invasive potential (Figure 4). We consider scenarios where FNN breadth mediates the ability of a propagule to sustain population growth when limited to food(s) of varying quality (Figure 4A–C)

nutrients and underingesting others when an animal is restricted to imbalanced diets that prevent it from reaching its intake target.

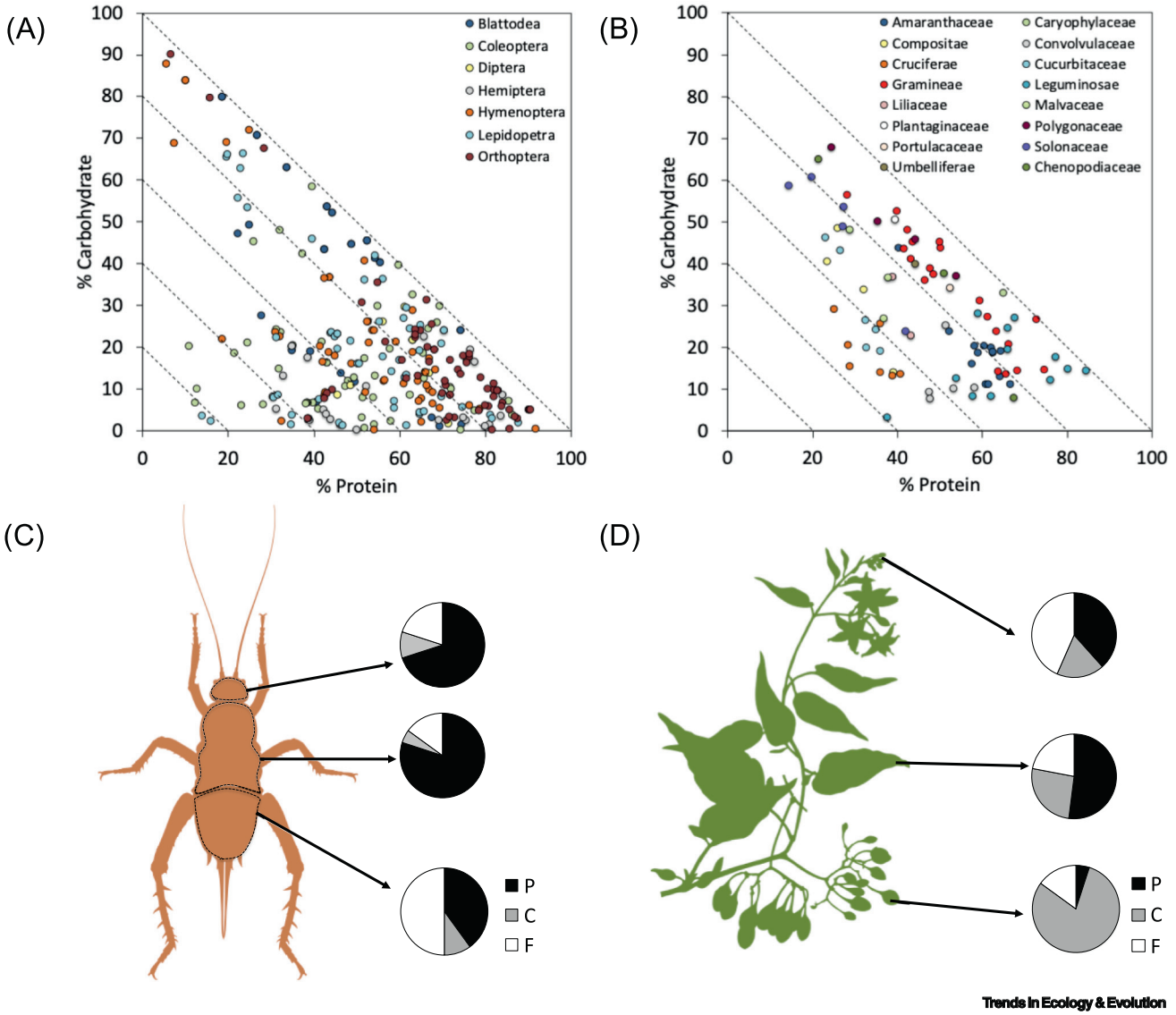

Figure 1. Taxonomically Similar Foods Can Have Different Nutritional Compositions. Food-level studies of diet breadth can provide limited predictions about invasive potential because foods are often decoupled from the fundamental nutritional niche (FNN) of an organism, and thus from the physiological mechanisms driving population growth following introduction. We highlight extreme variation in the relative amounts of fat (F), carbohydrates (C), and protein (P) in animal prey items and plant hosts, focusing on (A) common insect orders and (B) grasses, that would be consumed by a broad range of potential invasive species. This variation also occurs within single food items because (C) insect prey body parts and (D) plant structures are often composed of different blends of nutrients. Data from [117–122].

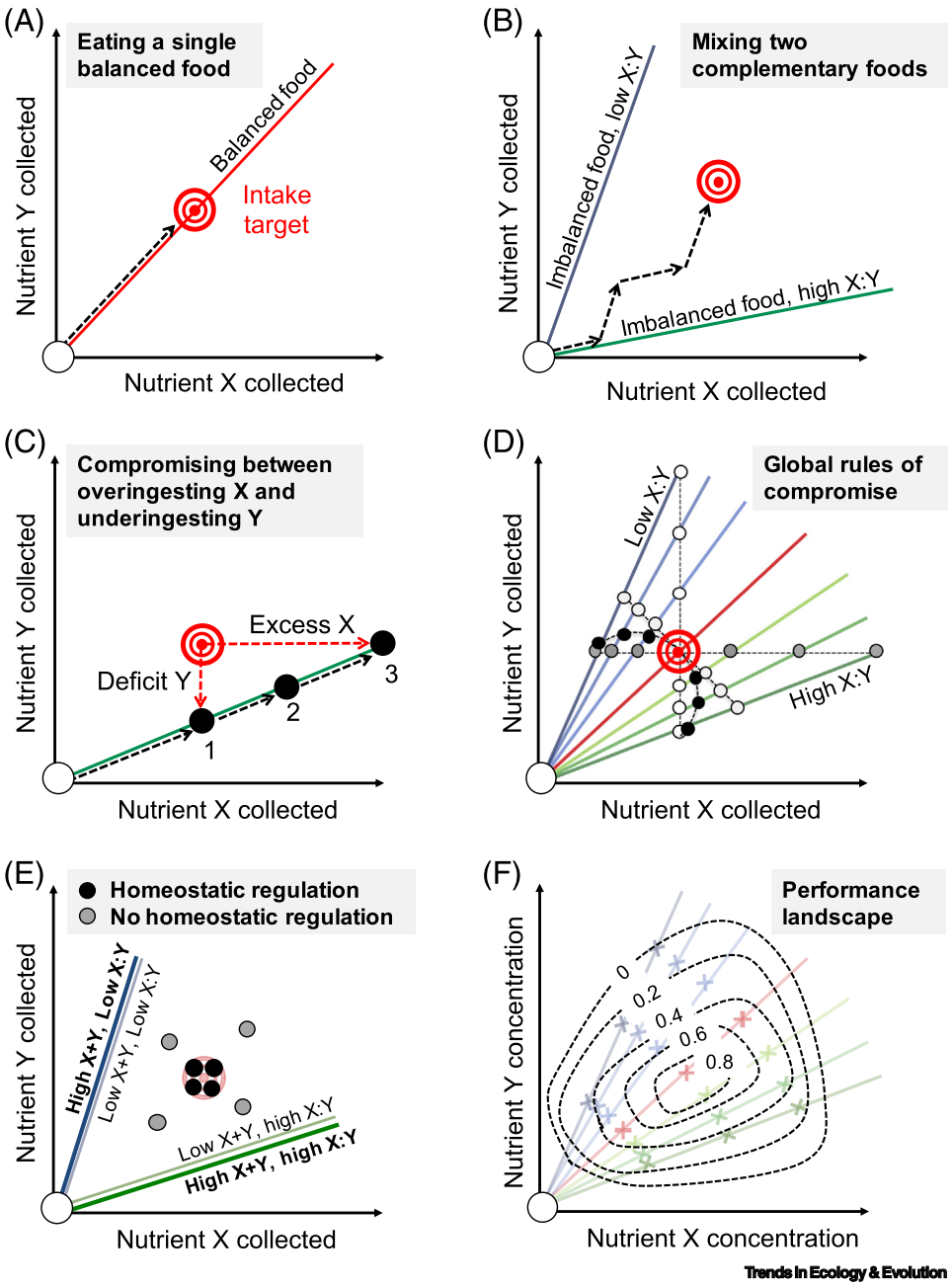

Figure 2. Nutritional Geometry Proposes a Nutrient Space Where the Axes Represent Food Components (X and Y). Foods are diagonal lines (nutritional rail) whose slopes indicates their X:Y nutritional balance, and a white dot indicates the initial nutritional state of an individual. (A) An animal reaches its intake target (IT, red bullseye) by eating a food whose X:Y ratio intersects with its IT. (B) An animal can reach its IT by foraging between an X-biased food (blue line) and a Y-biased food (green line). (C) When confined to an imbalanced food, an animal has three options: (1) undereating the food to regulate nutrient X (suffers a lack of Y), (2) compromising by reaching the closest distance to the IT, or (3) overeating the food to regulate nutrient Y (ingests an excess of X). (D) Animals can exhibit many potential rules of compromise when confined to single foods that vary in their X:Y ratio, ranging from a Y-biased food (dark-blue line) to an X-biased food (dark-green line). Foraging responses range from minimizing the distance from the IT (closest distance rule,

(Figure legend continued at the bottom of the next page.)

and relative abundance (Figure 4D,E), and when overcoming a state of initial nutritional imbalance following a stressful transport phase (Figure 4F).

We generated these predictions by performing an extensive literature review of the nutritional ecology of all animal species on the Global Invasive Species Database list of the 100 worst invaders (Table S1 in the supplementary material online). Traits related to nutrient acquisition, tolerance, and use have been extensively reviewed in invasive plants [47–53], and will not be considered further here. In animals, we identified several traits shaping FNN breadth that are commonly found in invasive species on the GISD list: generalist diet, opportunistic feeding, tolerance for nutrient scarcity or excess, physiological and behavioral flexibility to store, acquire and use nutrients efficiently, as well as diet switching and compensatory feeding (Table S1). Together these traits suggest that a broad FNN (relative to the FNNs of closely related species with low invasive potential) is a key trait that enhances invasive potential (Table S1). It will become increasingly possible to evaluate this core prediction as more researchers perform NG analyses of species spanning a continuum of invasive potential, including failed propagules.

Invasive potential can be predicted from the multidimensional nutritional niche of an animal [8], where broad FNNs enable propagules to overeat imbalanced foods and gain limiting nutrients at the cost of overeating other nutrients. We first posit a propagule introduced into a new environment with access to a single food whose nutritional balance is defined by an X:Y ratio of nutrients (Figure 4A). We represent foods with excess of nutrient Y using blue-shaded rails, and foods with excess of nutrient X using green-shaded rails. Successful invaders often freely consume less-suitable foods whose nutritional rails are farther from their intake targets. For instance, feral cats (*Felis catus*) overingest protein to maintain a balance of carbohydrates and fat [54], whereas larvae of the gypsy moth (*Lymantria dispar*) overeat carbohydrates to acquire protein [55], and invasive ants often overeat protein to secure sufficient carbohydrates [56]. Noninvasive species such as the mountain gorillas (*Gorilla beringei*) [57] and the black garden ant (*Lasius niger*) [58] are also known to overeat imbalanced foods to secure limiting nutrients, but to a much lower extent than species with high invasive potential. For instance, successful invaders constrained to eat imbalanced foods with extreme macronutrient ratios often maintain constant nutrient intake regardless of the X:Y ratio of the food (i.e., the equal distance rule). Examples include the slider turtle (*Trachemys scripta elegans*) [59], Nile perch (*Lates niloticus*) [60], red deer (*Cervus elaphus*) [61], walking catfish (*Clarias batrachus*) [62], and rhesus monkey (*Macaca mulatta*) [63].

Diverse physiological and behavioral traits account for the broad **nutrient tolerance** that accompanies high invasive potential, and include long-term survival on diets ranging widely in fat (F) and carbohydrate (C) content (from 0.02 to 40 F:C) in the walking catfish [64], as well as thriving when dietary protein ranges from an excess of 15% to a deficit of 24% relative to the intake target in the Chinese hairy crab (*Eriocheir sinensis)* [65–68]. Other invaders, such as gypsy moths [55] and largemouth bass (*Micropterus salmoides*) [69,70], thrive when confined to foods across many imbalanced macronutrient treatments. Others thrive despite consuming imbalanced blends of specific amino acids (largemouth bass [71]) and lipids that vary widely in fatty acid composition

black dots), maintaining a constant nutritional intake across foods (equal distance rule, light-grey dots), or maintaining constant intake of Y (grey dots) or X (white dots) regardless of the X:Y ratio. (E) Animals can feed indiscriminately regardless of food pairings (grey dots) or defend an IT by eating specific food proportions (black dots). This is assessed by offering a choice between a pair of foods that differ in composition (dark-blue and dark-green lines) and dilution (light-blue and light-green lines), in four dilution-pairing treatments. (F) Performance landscapes can be created by confining an animal to one of 21 diets that differ in their X:Y ratio (colored lines) and X+Y concentration (crosses). The isoclines (black broken lines) enclose areas where performance values (e.g., reproductive success) are similar and identify the region in nutrient space that maximizes the performance of the organism.

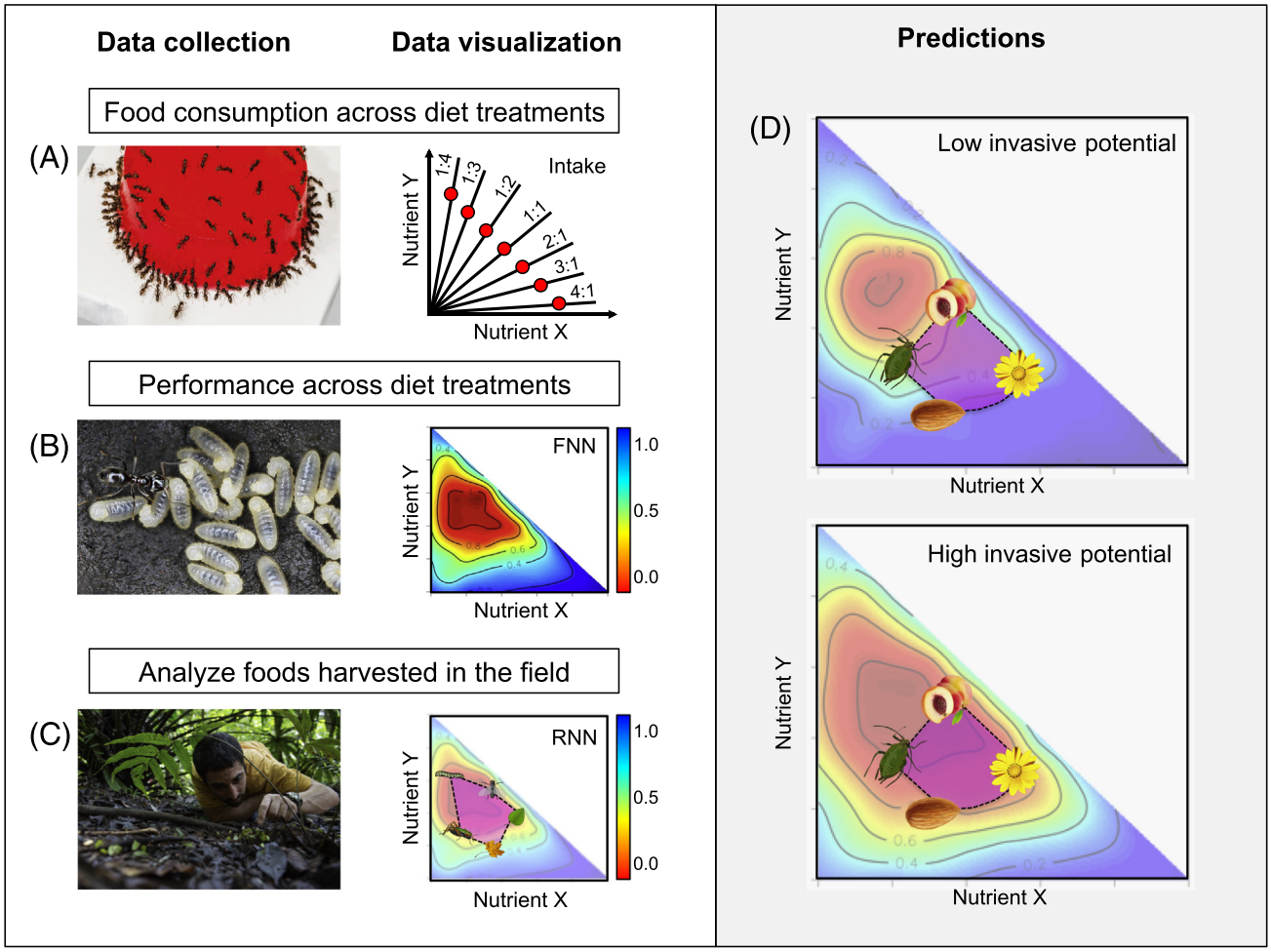

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Figure 3. How To Use Nutritional Geometry (NG) for the Study of Invasive Species. (A) The intake array. The first step is to confine the focal organism (e.g., ants) to a range of diets that differ in macronutrient composition (e.g., ratios of nutrients X:Y, here from 1:6 to 6:1). Diet intake is measured over a relevant period of time to define the rule of compromise. (B) The performance landscape. The organism is confined to a broader range of diets that differ in X:Y ratios and X+Y concentrations. Estimates of performance (e.g., survival, fitness) are measured for each diet treatment (black dot) to generate maps of fundamental nutritional niche (FNN) breadth. Red areas indicate the highest performance values on a response surface, and dark-blue areas indicate the lowest performance. (C) The foraging landscape. The organism is studied in the field where each food item it harvests is collected and catalogued by a researcher and analyzed to determine nutritional composition. The X and Y nutritional composition of each individual food item is then superimposed on the performance landscape to delimit the realized nutritional niche (RNN). (D) Predicting invasive potential. The overlap between the FNN and the RNN is assessed. Species with low invasive potential are predicted to have a narrow FNN because this provides limited opportunity to harvest suitable RNNs that maximize fitness in introduced habitats. By contrast, broad FNNs confer high invasive potential because the same RNN is more likely to facilitate high invasive performance.

(rainbow trout *Oncorhynchus mykiss* [72,73]). The invasive Formosan subterranean termite *Coptotermes formosanus* and Eastern subterranean [74] termite *Reticulitermes flavipes* can be maintained for months when fed a cellulose-only diet [75], whereas colonies of the non-invasive subterranean termite *Nasutitermes exitiosus* fed on a similar diet exhibit high mortality after 2 weeks [76].

We next consider a propagule that can access one diluted food with low total amounts of limiting nutrients, and predict that a species with high invasive potential can overeat such a low-quality food more quickly than a species with low invasive potential so as to reach its intake target in a single feeding event (Figure 4B). Diverse invaders readily overconsume diluted foods, including

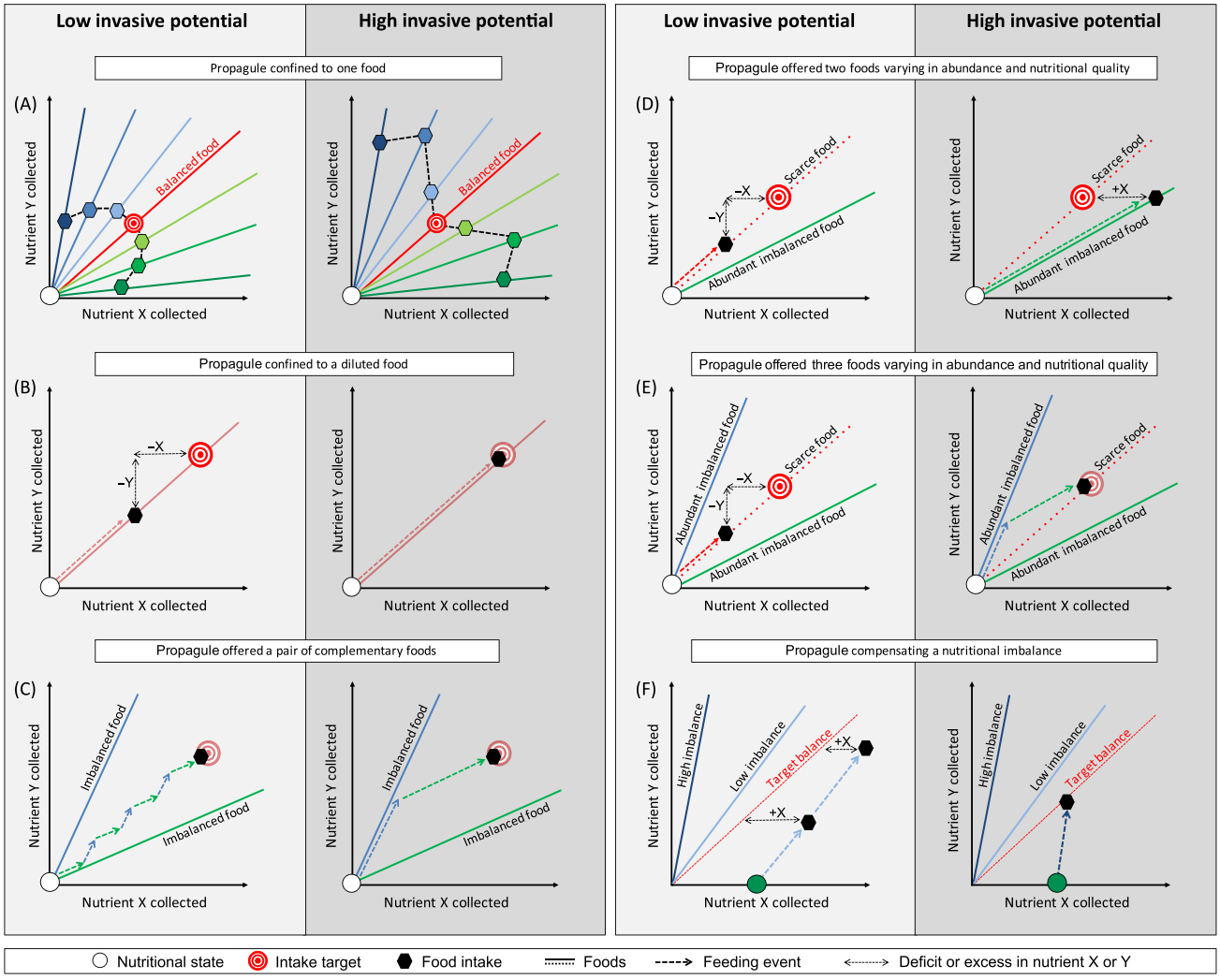

Figure 4. Predicting How Fundamental Nutritional Niche (FNN) Dimensions Shape the Foraging Behaviors of Successful Invaders. (A) When limited to imbalanced foods with an excess of nutrient Y (blue lines) or X (green lines), a species with low invasive potential (LIP) ceases foraging to avoid over consuming nutrients. A species with high invasive potential (HIP) forages to overconsume a nutrient relative to the intake target (IT, red bullseye) and thus acquires the other limiting nutrient. (B) When confined to nutritionally diluted foods, LIP species suffer limitation by failing to ramp up intake, whereas HIP species quickly reach their IT by eating more. (C) When confronted with two nutritionally imbalanced foods, LIP species prioritize staying close to their IT by frequently switching between these foods relative to HIP species. (D) When an environment provides a scarce balanced food and an abundant imbalanced food, LIP species preferentially forage on the scarce balanced food and suffer nutrient limitation, whereas HIP species consume the abundant imbalanced food, overingesting nutrient X but satisfying nutrient Y requirements. (E) In an environment that provides two abundant imbalanced foods and a scarce balanced food, LIP species preferentially search for the scarce balanced food, whereas HIP species more quickly reach their IT by switching between the two abundant imbalanced foods. (F) When a newly introduced propagule must overcome an imbalanced initial nutritional state (green circle), it must consume foods with high amounts of nutrient Y to quickly reach its IT. When confronted with two foods with different levels of X:Y imbalance, a LIP species eats only the more balanced food (light-blue line) and requires two meals to reach its IT, whereas a HIP species can rapidly reach its IT by consuming a single meal of the extremely imbalanced food (dark-blue line).

red deer [77], walking catfish [78], slider turtle [79], and the common carp (*Cyprinus carpio*) [80]. The invasive Argentine ant (*Linepithema humile*) can maintain constant nutrient intake across a wide range of nutrient dilutions after only 1 day of restriction [81], whereas noninvasive black garden ants show only a slight tendency to compensate nutrient dilution after 2 weeks [58].

Novel habitats often offer multiple foods, and we next posit a scenario where a propagule can approach its intake target by switching between two nutritionally imbalanced foods (Figure 4C). Diet switching likely imposes especially high costs during invasive establishment when propagules can scarcely afford to expend time and energy in finding new food patches. However, consuming a single imbalanced food is also physiologically costly. Broad FNNs are predicted to enhance invasive potential by decreasing these physiological costs, thus reducing the need to switch foods. Delayed diet switching from day to night has been observed to reduce predation risk in the invasive Mozambique tilapia (*Oreochromis mossambicus*) [82], and the invasive ctenophore *Mnemiopsis leidyi* can remain feeding at a patch for months [83,84].

Foods in introduced habitats likely vary in both their nutritional quality and relative abundance. We next consider an environment that provides an abundant imbalanced food and a rare balanced food (Figure 4D). Species with high invasive potential will thrive by maximizing total caloric intake while consuming the abundant low-quality food, instead of being confined to a high-quality food that is hard to find (Figure 4D). Examples of this include invasive brown trout (*Salmo trutta*) that consumes the most abundant prey items regardless of their nutritional quality [85], the coypu (*Myocastor coypus*) that copes with food scarcity by switching from carbohydrate-rich plant roots to abundant tree bark despite its nutritional imbalance [86], and Argentine ants that focus most of their foraging activity on periodically available but highly abundant carbohydrate-biased resources [87]. In addition, invasive red deer likely gain a competitive edge by prioritizing abundance over quality because they thrive while consuming many imbalanced foods (e.g., pine needles, tree bark [88,89]), whereas native competitors rely on a lower number of high-quality foraging patches [90].

We next extend this example to consider when propagules can access two abundant low-quality foods and one scarce high-quality food (Figure 4E). Species with high invasive potential can quickly reach their intake target by switching between the complementary imbalanced foods instead of slowly inching towards the target by consuming small or intermittent meals of a high-quality rare food (Figure 4E). Complementary food switching in response to food scarcity has been observed in the zebra mussel (*Dreissena polymorpha*) that alternates between seston and detritus when access to phytoplankton is limited [91], as well as in Nile perch in Lake Victoria that switched from increasingly rare cichlids to aquatic invertebrates and other fish taxa [92]. Dramatic relaxation of food selectivity during periods of scarcity has also been observed in the rat (*Rattus rattus*) [12], macaque (*Macaca fascicularis*) [93,94], fox (*Vulpes vulpes*) [95], and mosquitofish (*Gambusia affinis*) [96].

Introduced propagules often arrive in new habitats following a stressful period of transport [97], even if transport distances are shortened by bridgehead effects [98]. Transported propagules likely face prolonged confinement to nutritionally imbalanced foods that bias their nutritional state upon arrival (Figure 4F). We consider a scenario in which the transported propagule has been confined to a food with an excess of nutrient X, and must quickly redress its nutritional imbalance and reach its intake target by consuming a complementary food containing an excess of nutrient Y (Figure 4F). A species with high invasive potential will more rapidly recover a balanced nutritional state by consuming an extremely Y-biased food (dark-blue line), whereas a species with low invasive potential will be confined to a more balanced X:Y food (turquoise line) and thus require more successive meals to reach its intake target (Figure 4F). This has been observed in invasive Argentine ants that can quickly harvest extremely complementary foods to recover from deprivation of carbohydrates, sterols, proteins, and even a subset of amino acids [99]. Similar responses involving different types of nutrient overconsumption have been observed in feral cats [54], Minas (*Acridotheres tristis*) [100], feral pigs (*Sus scrofa*) [101], and rainbow trout [102].

Nutritional Dimensions Governing Long-Term Invasive Success

We next extend NG predictions to longer-term phases of invasive establishment. In this case propagules must overcome physiological constraints imposed by FNN dimensions inherited from the native range that may be mismatched for newly available foods and narrowed by bottlenecks in founding populations. We compare the invasive potential of three hypothetical species that exhibit similar native-range RNNs but have FNNs ranging from narrow (species A) to broad in terms of nutrient X (species B) or nutrient Y (species C) (Figure 5). We propose a scenario

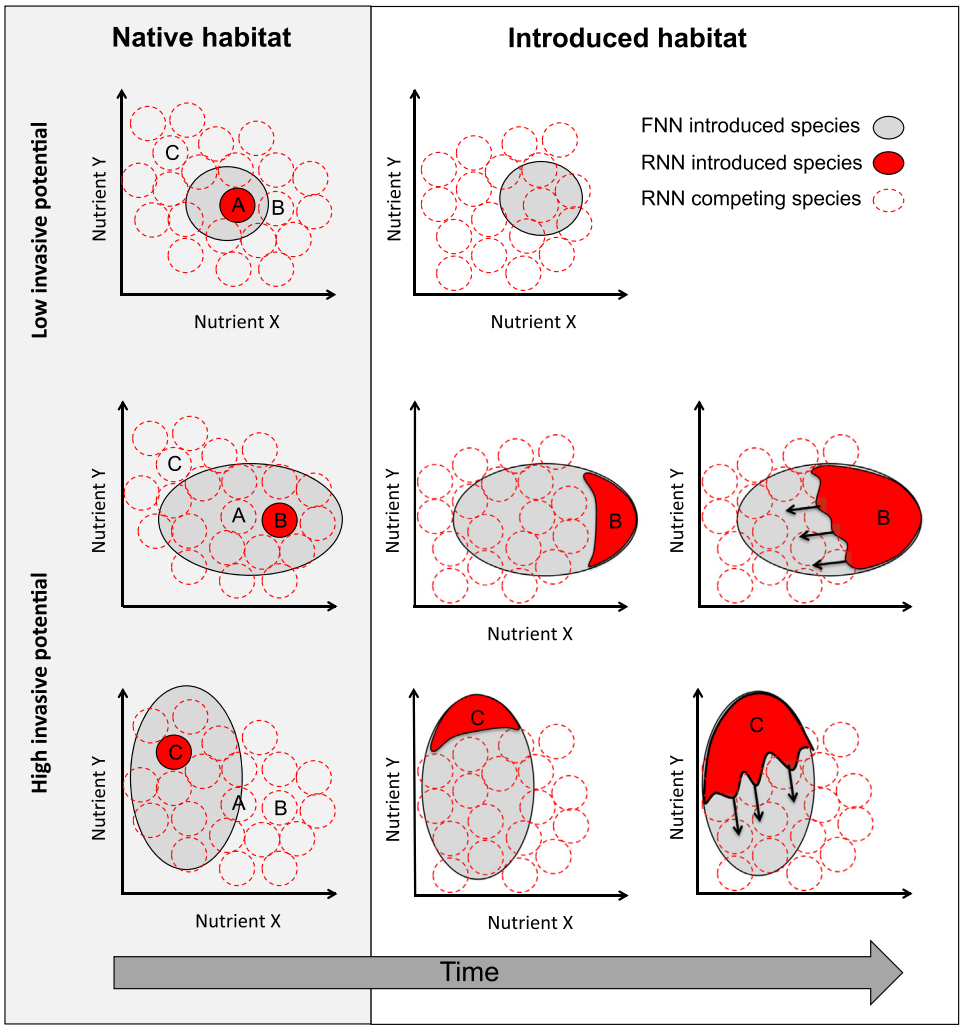

Figure 5. Predicting Nutritional Dimensions Governing Long-Term Invasive Success, Based on Fundamental Nutritional Niche (FNN) Dimensions Observed in the Native Range. These examples consider communities where the coexistence of resident species is mediated by nutritional niche partitioning, and where high species diversity presents barriers to invasion. Hypothetical species A has a narrow FNN and thus has low invasive potential because it will be unable to acquire foods that provide a realized nutritional niche (RNN) suitable for sustaining population growth. Species B and C have higher invasive potential because their broad FNNs enable their initial survival at the nutritional margins, until they ultimately outcompete native residents through a combination of life-history traits and behavioral mechanisms, as outlined in Figure 4. This example also shows that broad FNNs provide alternative routes to invasive establishment for species B (tolerance to variation in nutrient X) and C (tolerant to variation in nutrient Y), and that RNNs measured in native habitats are not sufficient to predict invasive potential and should be combined with FNN measurements (Figure 3B).

whereby propagules A, B, and C enter a community in which the coexistence of resident species is mediated by nutritional niche partitioning, such that much of the available **nutritional landscape** is already monopolized, as predicted by the biotic resistance hypothesis [103] (Figure 5).

Species A has low invasive potential because its narrow FNN makes it unable to acquire the nutrients it needs to sustain population growth (Figure 5). By contrast, broad FNNs enable species B and C to gain initial nutritional footholds even if their RNNs are severely restricted relative to what could be acquired in the respective native ranges (Figure 5). These links between FNN performance breadth and RNN foraging breadth can be visualized by comparing an ant species with low invasive potential, the black garden ant (*Lasius niger*) [58], with two species with high invasive potential, the Argentine ant [81] and the pharaoh's ant (*Monomorium pharaonis*) [104] (Figure S1). Once established, species B and C continue to dominate nutritionally marginal foods for which there is little competition, while also outcompeting native species through the behavioral mechanisms outlined in Figure 4. This example also highlights that RNNs must be combined with FNNs to predict invasive potential because species A has lower invasive potential than B or C despite having native-range RNNs of similar dimensions (Figure 5).

Concluding Remarks and Further Applications

By using NG to define food-level studies in terms of fundamental and realized nutritional niches, we provide three keys to dramatically increase predictive power in the field of invasive species biology. First, nutritionally explicit approaches provide clear links to the physiological mechanisms that govern invasive potential, including post-ingestive regulatory mechanisms (e.g., nutrient assimilation or excretion) that enable nutrient overingestion. Comparative genomics approaches across gradients of invasive potential can further reveal general features of the metabolic pathways that govern FNN breadth. Convergent adaptations that regulate other forms of nutritional tolerance can also be revealed, including extreme starvation resistance that is common among the most notorious invaders (Table S1). Many invaders are also actively cultivated through applied animal husbandry, and NG can integrate the responses of ecologists to the global threat of species invasions with applied research designed to maximize yield, thereby unlocking a wealth of new nutritional insights (Table S1).

Second, NG is a rapidly emerging field that will continue to produce new theory and practical tools for studying invasive species. For instance, nutritional landscape dimensions can now include three interacting nutrients by using right mixture triangle approaches [104–106] while also tackling pressing issues of public health [39]. This toolbox can also probe more complex evolutionary dynamics because the breadth of the FNN of an organism is undoubtedly a labile trait [107,108] that is shaped by a complex network of local adaptation, developmental plasticity, learning, epigenetics, and microbiome composition [6,109]. For instance, we can use NG to understand the physiological and behavioral mechanisms that make successful invaders good at monopolizing food resources such as growth rate, photosynthetic rate, leaf construction cost, leaf area and shoot allocation, and allelopathy in plants [52], as well as an advanced capacity for learning, innovation, aggressiveness, and host manipulation in animals [110,111].

Third, additional ecophysiological mechanisms can be more explicitly integrated into NG models because invasive FNN and RNN breadth also depend on abiotic factors including thermal tolerance [112,113] and physiological interactions with symbionts such as gut-inhabiting bacteria [74,114,115]. Fascinatingly, bacterial endosymbionts can also shape thermal [116] and nutritional niche breadth [74,114,115] in their hosts, thus providing exciting additional possibilities to achieve truly integrative mechanistic predictive power using NG approaches (see Outstanding Questions).

Outstanding Questions

Can we extend laboratory experiments with nutritionally defined diets beyond two nutritional dimensions to strengthen predictions about invasive potential?

What performance currencies will be most useful, practical, and general in comparing fundamental nutritional niches across diverse species representing a broad continuum of invasive potential?

What are the most widespread nutritional tradeoffs faced by invasive species, and to what extent have convergent patterns of genomic evolution enabled successful invaders to overcome these tradeoffs?

Can we place diverse species on a continuum of invasiveness by analyzing nutrients in the foods that they harvest in the field?

How does the identity of limiting nutrients and the nature of nutritional tradeoffs change across stages of invasions?

Do broad fundamental nutritional niches enable broad realized nutritional niches, and does this linkage predict invasive potential?

Can the explicitly nutritional approach provided by NG reveal general physiological mechanisms governing invasive potential?

How can NG approaches be most effectively integrated with other niche dimensions that govern invasive potential, such as thermal tolerance, and how are niche dimensions mediated by microbial symbionts?

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